

Accounting for demographic and environmental stochasticity,
observation error and parameter uncertainty in fish population
dynamics models

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Abstract

Bayesian hierarchical state-space models are a means of modeling fish population dynamics while accounting for both demographic and environmental stochasticity, observation noise, and parameter uncertainty. Sequential importance sampling can be used to generate posterior distributions for parameters, unobserved states, and random effects for population models with realistic dynamics and error distributions. Such a state-space model was fit to the Sacramento River winter chinook salmon (*Oncorhynchus tshawytscha*) population where a key objective was to develop a tool for predicting juvenile outmigration based on multiple sources of data. One-year-ahead 90% prediction intervals based on 1992-2003 data, while relatively wide, did include estimated values for 2004. Parameter estimates for the juvenile production function based on the state-space model formulation differed sizeably from Bayesian estimates that ignored autocorrelation and observation noise.

Key words: chinook salmon, endangered species, forecasting, sequential importance sampling, state-space model.

1 Introduction

Variation in the numbers, age and sex structure in an animal population can be viewed as a function of stochastic processes that include survival, maturation, reproduction, harvest, and movement (Caswell 2001). For many animal populations, the numbers in each stage cannot be measured exactly and information about abundance and structure is based on sample surveys and, in the case of harvested fish populations, catch data. The resulting two, potentially multivariate, time series, one representing the true but unobservable population structure and the other the observed data, can be modeled using a state-space model (SSM) (Harvey 1989). We will call the development or evolution of the population structure the state process and the measurements taken on the populations the observation process (Buckland et al. 2004).

A more mathematical definition of a SSM is given later but here we discuss some general issues. State-space models can be used to provide three kinds of inference. One is to estimate the unobserved population structure given the observed data and another is to estimate parameters that characterize the state and observation processes. In the case of fish populations such parameters can include vital rates (survival, fecundity, and maturation), harvest rates, and movement probabilities in the case of spatially structured populations. A third inferential objective is to predict future population values.

An advantage of SSMs is that they can account for several distinct types of randomness or uncertainty in the state and observation processes. Ignoring sources of uncertainty can lead to overly optimistic assessments of the overall uncertainty of inferences. There is demographic uncertainty: for a particular set of parameters, say vital rates, and a given population structure at time t , the population structure at time $t+1$ varies at random; e.g., given 100 individuals alive at time t with a survival rate of 0.8, the observed number alive at time $t+1$ could be 77, 80, 83, etc. There is environmental stochasticity: the parameters themselves

1 are stochastic, varying with time, with environmental conditions; e.g., survival rates are on
2 average 0.8 but vary stochastically from 0.6 to 0.9, say. There is parameter uncertainty: the
3 parameters are usually never known with certainty and must be estimated from observable
4 data. There is observation or measurement error: observations or estimates of states rarely
5 equal the true state values. Lastly there is model uncertainty: the structural form for the
6 state and observation processes is at best an approximation to reality and alternative (still
7 approximate) models could have been used.

8 We fit a Bayesian hierarchical state-space model to model the population dynamics of the
9 Sacramento River winter run chinook salmon population. The model accounts for four of the
10 above types of uncertainty, excluding model uncertainty since just a single model was con-
11 sidered. Sacramento River winter chinook salmon (*Oncorhynchus tshawytscha*) population
12 levels have severely declined during the 20th century due to blockage of historical spawning
13 areas by Shasta Dam, extensive degradation of remaining spawning, rearing and migration
14 habitats, and overfishing (NMFS 1997) (Figure 1). Estimates of winter run returns to Red
15 Bluff Diversion Dam (RBDD) (rkm 391) decreased from 117,800 in 1969 to 1,156 in 1980,
16 which led to the stock being placed on the United States endangered species list in 1994.
17 Subsequent management actions to try to increase the stock's abundance include changes in
18 ocean fishing regulations, operations of Red Bluff Diversion (a partial barrier to fish passage
19 when in operation), numerous habitat restoration actions, and regulation of certain other
20 activities that potentially harm winter chinook.

21 Estimates of juvenile salmon numbers are a crucial component of management of the win-
22 ter run. One of the management actions taken to increase abundance has been to regulate
23 water export during the period of juvenile winter chinook salmon outmigration. The two
24 largest water export facilities are the State Water Project's Harvey Banks Delta Pumping
25 Plant (SWP) and the Central Valley Project's Tracy Pumping Plant (CVP). The opera-
26 tors of the pumps attempt to keep entrainment-related mortality below levels specified as a

1 fraction of the predicted number of juvenile winter-run chinook salmon. Predictions of juve-
2 nile abundance have been made using models based upon prior year escapement estimates,
3 in-river samples of juveniles during outmigration, and samples of juvenile salmon taken at
4 SWP and CVP (Snider and Titus 2000; Martin et al. 2001). To date, the accuracy of predic-
5 tions and how best to combine information from multiple sources has not been adequately
6 addressed.

7 The next section describes our methodology including a more formal description of
8 Bayesian hierarchical SSMS, background information and data for the winter run salmon,
9 and the sequential importance sampling procedure used for making inferences. The results
10 are next and are followed by discussion.

11 **2 Methods**

12 **2.1 Bayesian hierarchical state-space models**

13 Let \mathbf{n}_t denote a vector of abundances of a population at time t where the elements of the
14 vector are numbers distinguished by particular attributes, e.g., age and sex, and let \mathbf{y}_t denote
15 a vector of measurements or data where the components are a function of \mathbf{n}_t . We will call
16 \mathbf{n}_t the state vector and \mathbf{y}_t the observation vector. To keep the notation simple we assume
17 that $t=0,1,\dots,T$, where T is an integer; thus the time series is regularly spaced. Irregularly
18 spaced time series can be readily handled as well. A state-space model is a model describing
19 the evolution of the two time series, \mathbf{n}_t and \mathbf{y}_t , where \mathbf{n}_t is first-order Markov, i.e., given all
20 previous state vectors the conditional probability distribution for \mathbf{n}_t is a function of just \mathbf{n}_{t-1} ,
21 and the probability distribution for \mathbf{y}_t is expressed as a function of \mathbf{n}_t . More succinctly, a
22 non-hierarchical SSM can be characterized in terms of probability density or mass functions

1 (pdf's):

2 Initial state pdf : $g_0(\mathbf{n}_0, \theta)$

3 State process pdf : $g_t(\mathbf{n}_t | \mathbf{n}_{t-1}, \theta)$

4 Observation process pdf : $f_t(\mathbf{y}_t | \mathbf{n}_t, \theta)$,

5 where θ is a vector of time invariant parameters for the state and observation processes which
6 can include vital rates and observation variances, for example.

7 In the above formulation the parameters θ are assumed constant or time invariant. Thus
8 the formulation reflects demographic stochasticity and observation uncertainty. Environ-
9 mental stochasticity is added by allowing at least some of the components of θ to vary with
10 time, say $\theta_t = (\psi_t, \eta)$, where ψ_t are time varying. Another pdf, $h(\psi_t | \Gamma)$, is added to describe
11 the variation in ψ_t , where Γ is a vector of hyperparameters and h is sometimes referred to
12 as a hyperdistribution. The resulting model is a hierarchical SSM (Newman 2000; Rivot et
13 al. 2004).

14 *A priori* uncertainty about parameters, including hyperparameters, and state values is
15 specified by means of prior distributions. Prior distributions for all states are implicitly
16 defined given priors for θ and \mathbf{n}_0 alone. The combination of prior distributions, the hyper-
17 distribution for parameters, and the state-space model is a Bayesian hierarchical state-space
18 model, which we summarize as follows.

19 Prior pdfs for parameters : $\pi(\eta, \Gamma)$ (1)

20 Hyperdistribution pdf : $h(\psi_t | \Gamma)$ (2)

21 Initial state pdf : $g_0(\mathbf{n}_0 | \theta_0)$ (3)

22 State process pdf : $g_t(\mathbf{n}_t | \mathbf{n}_{t-1}, \theta_t)$ $t = 1, 2, \dots, T$ (4)

23 Observation process pdf : $f_t(\mathbf{y}_t | \mathbf{n}_t, \theta_t)$, $t = 1, 2, \dots, T$. (5)

1 Inference about the states and parameters is made conditional on the observations. All
 2 relevant information can be found from the posterior distribution for the states and param-
 3 eters, namely,

$$4 \quad \pi(\mathbf{n}_{0:T}, \eta, \Gamma, \psi_{0:T} | \mathbf{y}_{1:T}) \propto \pi(\eta, \Gamma) h(\psi_t | \Gamma) g_0(\mathbf{n}_0, \theta_t) \prod_{t=1}^T g_t(\mathbf{n}_t | \mathbf{n}_{t-1}, \theta_t) f_t(\mathbf{y}_t | \mathbf{n}_t, \theta_t), \quad (6)$$

5 where the subscripts $(0 : T)$ and $(1 : T)$ denote a sequence of values from 0 to T or 1 to T .
 6 In the state-space modeling literature inferences about the states made conditional on the
 7 *entire* time series of observations is known as smoothing, whereas inference about the state
 8 at time t , \mathbf{n}_t , based on data just up to time t , $\mathbf{y}_{1:t}$, is known as filtering.

9 Calculation of the posterior distribution is analytically intractable in most situations and
 10 simulated inference procedures such as MCMC (Gilks et al. 1996) or sequential importance
 11 sampling (SIS) (Liu and Chen 1998) are used instead. For the application to salmon we use
 12 a variation on SIS (Liu and West 2001) and describe the details of the implementation later.

13 **2.2 Winter chinook salmon life history**

14 The state process pdf used in the SSM is based on a model for the life history of winter
 15 chinook salmon and we provide some background on the life history before presenting a
 16 mathematical formulation.

17 The life history of Sacramento River winter chinook is unique among chinook salmon
 18 (Healey 1991). Maturing fish enter freshwater in winter and migrate far upstream, where
 19 they spawn in late spring. Eggs incubate during the summer, and juveniles begin migrating
 20 downstream in the fall, and they enter the ocean before the following summer. Juveniles
 21 spend one to three summers at sea before returning to spawn. We model this life history
 22 on a relatively coarse annual scale (see Figure 2). Let t denote the time index for a given
 23 annual period, where increments to the index are between the end of the escapement period
 24 and the beginning of the period of juvenile outmigration (late summer). In a given year

1 the abundances of the salmon are distinguished by eleven distinct and non-overlapping cat-
 2 egories: outmigrating juveniles (J_t), immature ocean dwelling fish (O_{ast}), and adult returns
 3 or escapement (S_{ast}), where a denotes age (2, 3, or 4) and s denotes sex (m,f).

4 The life history of a year t cohort begins with the juvenile freshwater stage. Survivors
 5 to year $t+1$ are partitioned into four sex and maturation categories: $O_{2m(t+1)}$, $O_{2f(t+1)}$,
 6 $S_{2m(t+1)}$, $S_{2f(t+1)}$. For year $t+2$, survivors from the previous year's ocean residents are again
 7 partitioned into immatures and escapement. The final year of the cohort is $t+3$ and it
 8 contains the prior year's ocean survivors who then (are assumed to) mature with certainty.

9 In Figure 2 a schematic of the life history of a *given* cohort is shown. The model pa-
 10 rameters are related to the three stochastic processes of birth, survival, and maturation.
 11 The birth parameters (not shown in Figure 2) include productivity and density dependent
 12 parameters, as well as a variance parameter reflecting stochastic variation in reproductive
 13 success. The parameters ϕ_a ($a=2,3,4$) are the expected annual survival rates from age $a - 1$
 14 to a , p_m is the proportion of males, and ρ_{as} is the expected probability of an age a , sex s
 15 fish maturing. The survival probabilities include natural and fishing mortality, but due to
 16 the endangered status of the stock and the fact that current ocean fisheries' management is
 17 designed to minimize impact on winter chinook salmon, fishing mortality is believed to be
 18 small relative to natural mortality. In the absence of sizeable CWT recovery information,
 19 and a model that links fishing effort or season length to harvest rate, the ϕ_a 's cannot be
 20 meaningfully partitioned into natural survival rates and fishery survival rates.

21 The schematic in Figure 2 does not make explicit two potentially important mortality
 22 processes, mortality of juveniles at the export pumps (especially CVP and SWP) and ocean
 23 harvest. Because of these sources of mortality and variation in fisheries' effects, survival and
 24 maturity parameters vary between years, a reflection of environmental stochasticity; i.e.,
 25 more accurate notation is ϕ_{at} and ρ_{ast} . Pump-related mortality is absorbed in the ϕ_{2t} term.

2.3 Data

Data for winter run chinook salmon come from samples taken of freshwater juveniles and mature freshwater returns (Table 1). The juvenile data arise from in-river sampling; for seven of nine years between 1996 and 2004, rotary screw traps were placed directly behind Red Bluff Diversion Dam (Martin et al. 2001; Gaines and Poytress 2004) to collect samples of outmigrating juvenile salmon in the Sacramento River. Chinook salmon of different races (winter, spring, fall, and late-fall) were recovered by the traps and identification of juveniles as to race was inexact, based largely upon classification rules that are functions of fish length and time of year and partially upon coded-wire tag information, the latter coming from releases from Livingston Stone National Fish Hatchery. Juvenile abundance is estimated in terms of fry equivalents (Martin et al. 2001) and estimates are essentially stratified random sample expansions of weekly estimates, which in turn are based on a model for trap efficiency as a function of water flow. Trapping takes place over several months and over time fish mature to become pre-smolts and smolts. Pre-smolts and smolts (defined to be $> 45\text{mm FL}$) are multiplied by a factor of 1.69 to become fry equivalents. Such a conversion of pre-smolts and smolts to fry introduces additional error into the estimates since pre-smolts and smolts recovered late in the outmigration period are presumably a smaller fraction of surviving fry than are pre-smolts and smolts recovered early in the outmigration period. Also relevant to juvenile production is the fact that since 2002 the number of hatchery-reared females (from Livingston Stone Fish Hatchery) spawning naturally in the river, so-called hatchery strays, has increased enough that their contribution to juvenile production may be non-ignorable.

There are two primary sources of adult return data, ladder counts at Red Bluff Diversion Dam combined with recoveries at a fish trap by the dam and female carcass mark-recovery data (Killam and Harvey-Arrison 2005). Ladder counts have been made since 1967. Multiple races of chinook salmon return to the dam and separation of races is based on time of year

1 and phenotypical characteristics of trap-captured salmon (including color, scale condition,
2 and relative degree of sexual maturation, (Killam and Harvey-Arrison, 2005)). Beginning
3 in 1986, the operational period of the ladder during the winter chinook salmon migration
4 period was greatly reduced and the operational period since then is estimated to cover the
5 last 15% of the migration period (from week 20 through week 37). The estimated winter
6 chinook salmon escapement for 1986 on then is calculated by multiplying the total ladder
7 counts during the observation period by fish trap-based proportion of winter chinook salmon
8 and then dividing by 0.15. The 15% figure is based on data collected during the last five
9 years of continuous ladder operation. Given that the standard deviation of the fractions seen
10 after week 20 is 0.187, it can be shown analytically that the expected coefficient of variation
11 in the estimated total return based on the expanded ladder counts is around 125% . Using
12 the fish trap data, the estimated return to RBDD is further partitioned by sex and age class
13 (Doug Killam, personal communication). There are two assigned age classes, age 2 and ages
14 3 and 4 combined, and assignment is based on length (fish less than 61 cm FL are assigned
15 age 2).

16 The carcass mark-recovery (M/R) data have been used to make a Jolly-Seber estimate
17 of female adult returns for the years 2001-2004 (Killam and Harvey-Arrison 2005). Similar
18 to the RBDD estimates, the M/R estimates are partitioned into two age classes, age 2 and
19 ages 3 and 4 combined. The M/R estimates of female returns are consistently higher than
20 the corresponding RBDD estimates, but standard errors have not been calculated for either
21 set of estimates. The Jolly-Seber estimates have become the official figures used by the
22 California Department of Fish and Wildlife since 2001, but the RBDD estimates are still
23 calculated to maintain continuity of the data base and to detect long term trends.

24 A final item of data used for the modeling is a fecundity-length function estimated from
25 a sample of female returns (Frank Fisher, personal communication).

2.4 Chinook salmon SSM

The different components of the Bayesian hierarchical SSM are first described individually. Table 2 summarizes the SSM in terms of pdfs and parallels the general formulation shown in equations (1)-(5).

State process

There are eleven components in the state vector, \mathbf{n}_t , and they are the abundances of different ages and stages comprising the population mentioned previously:

$$\mathbf{n}'_t = (J_t, O_{2ft}, S_{2ft}, O_{2mt}, S_{2mt}, O_{3ft}, S_{3ft}, O_{3mt}, S_{3mt}, S_{4ft}, S_{4mt}),$$

Thus the state vector includes contributions from four successive cohorts, they are progeny of spawners in years $t-4$, $t-3$, $t-2$, and $t-1$. The pdf $g_t(\mathbf{n}_t|\mathbf{n}_{t-1})$ is vector-valued with six independent pdfs for the following sets of components: J_t , $(O_{2ft}, S_{2ft}, O_{2mt}, S_{2mt})$, (O_{3ft}, S_{3ft}) , (O_{3mt}, S_{3mt}) , S_{4ft} , and S_{4mt} . The sex ratio amongst juveniles was assumed 1:1.

The deterministic structure for J_t was a Beverton-Holt stock and recruitment model expressed in terms of egg production as a function of female returns, with a distinction made between eggs produced by age 2 females (assumed less than 61 cm FL) and eggs produced by ages 3 and 4 females. Mathematically,

$$E[J_t] = \frac{F_{t-1}\alpha}{1 + \beta F_{t-1}},$$

$$F_t = (S_{2f,t-1} + H_{2f,t-1}) \times \bar{E}_2 + (S_{3f,t-1} + S_{4f,t-1} + H_{3+4f,t-1}) \times \bar{E}_{3,4},$$

where $\bar{E}_2=3205$ and $\bar{E}_{3,4}=6304$ are the estimated average number of eggs for females less than 61 cm FL and greater than or equal to 61 cm FL, respectively. $H_{2f,t-1}$ and $H_{3+4f,t-1}$ are the estimated number of age 2, and ages 3 and 4 combined, hatchery strays. The stochastic formulation was a discretized bias-corrected lognormal distribution with coefficient of variation CV_{BH} . Note, if $Y \sim \text{Lognormal}(\mu, \sigma^2)$ where $\sigma^2 = \log(CV^2 + 1)$, then $\sqrt{\text{Var}(Y)}/E(Y) = CV$.

1 The age 2 components, $(O_{2mt}, S_{2mt}, O_{2ft}, S_{2ft})$, were assumed to be from a multinomial
2 distribution drawn from the previous years juveniles, J_{t-1} , where the parameters were a com-
3 bination of sex assignment (female with probability fixed at 0.5), survival, and maturation.
4 The survival and maturation parameters were random, reflecting environmental stochasticity
5 in addition to the demographic stochasticity characterized by the multinomial distribution.
6 Similarly the age 3 components, (O_{3mt}, S_{3mt}) and (O_{3ft}, S_{3ft}) , were generated from two tri-
7 nomial distributions drawn from the previous year's non-maturing age 2 males, $O_{2m,t-1}$, and
8 age 2 females, $O_{2f,t-1}$. Again survival and maturation rates were random. Likewise the age 4
9 components, S_{4mt} and S_{4ft} , were binomial random variables with the survival rate random.

10 **Hyperdistributions and prior distributions**

11 The survival and maturation rates are random effects and correspond to the ψ_t in equation
12 (2). Such values are necessarily restricted to $(0,1)$, and Beta distributions were used for
13 these rates. The parameters of the Beta distribution are themselves unknown values and
14 uniform prior distributions were used (i.e., these distributions correspond to $\pi(\cdot)$ in equation
15 (1)). The bounds of the uniform prior distributions were chosen such that the expected
16 values corresponded to values used previously (Newman et al. *in press*) and the coefficient
17 of variation was 50%.

18 Uniform priors were also used for the other, fixed effect parameters with the parameters
19 of the uniform in most cases chosen such that the expected values generally matched those
20 of priors used previously (Newman et al. *in press*).

21 Prior distributions for the initial states were generated from prior distributions for the
22 number of spawning females for the four years prior to 1992. From these spawning numbers
23 the number of juveniles, age 2, age 3, and age 4 fish could be progressively generated. Details
24 are shown in Table 2; Rivot et al. (2004) and Newman et al. (*in press*) describe essentially

1 the same approach to initialization.

2 **Observation process**

3 The observation vector had seven components which were the estimates of outmigrating
4 juveniles based on the rotary screw trap samples, the estimates of returning mature fish
5 distinguished by two age classes and sex based on the RBDD ladder counts and fish traps, and
6 the estimates of returning females distinguished by two age classes based on the carcass-based
7 M/R samples. Lognormal distributions were used for all the estimates with the assumption
8 that the estimates were unbiased for the unknown state values. For the RBDD ladder and
9 fish trap based estimates one coefficient of variation was assumed, $CV_{\hat{A}-RBDD}$, while different
10 coefficients of variation were used for the juvenile estimates, CV_j , and the M/R estimates of
11 female returns, $CV_{\hat{A}-M/R}$.

12 **2.5 Parameter and state estimation**

13 To generate samples from the posterior distributions for the states, parameters, and random
14 effects, a variation on sequential importance sampling, SIS, (Liu and Chen 1998) that com-
15 bines SIS with kernel smoothing of the parameters was used. The algorithm is given in Liu
16 and West (2001) and here we sketch the essentials of the implementation beginning with
17 an overview of the idea of SIS. We note that these inference procedures are also known as
18 particle filters or particle generators and the volume edited by Doucet et al. (2001) includes
19 many papers devoted to this subject.

20 We begin with the objective of generating a sample from a particular distribution, a
21 target distribution, with pdf $f(x)$. With importance sampling one generates a sample from
22 an “importance” distribution with pdf $\pi(x)$ which has support including that of $f(x)$. Denote
23 the generate sample values by x_i^* , $i = 1, \dots, N$. An (approximate) sample from $f(x)$ can be

1 generated by resampling the x_i^* 's, bootstrap resampling, with weights, w_i^* , proportional to
2 $f(x_i^*)/\pi(x_i^*)$. Such a procedure is sometimes referred to as Sampling Importance Resampling
3 or SIR (Rubin, 1988). The choice of the importance distribution affects the Monte Carlo
4 error, the variation between samples of the same size, and the closer $\pi(x)$ is to $f(x)$ the
5 smaller that variation (Ripley 1987).

6 In the case of state-space models, in particular, the target distribution is usually high
7 dimensional and finding a single importance distribution to generate the vector that will not
8 have large Monte Carlo error can be extremely difficult at best. SIS is a divide and conquer
9 solution to this problem: sequentially generate components of the target distribution using
10 importance sampling for each component and sequentially calculate the weights needed for
11 resampling. For example, consider a univariate SSM with T time periods. The objective is
12 to generate a sample from the smoothed distribution with pdf $g(x_{1:T}|y_{1:T}, x_0, \theta)$, where for
13 simplicity assume x_0 and θ are known. A sample value for x_1 is generated from a univariate
14 importance distribution with pdf $\pi_1(x_1)$ and a weight $w_1(x_1)$ is calculated from $\frac{f(y_1|x_1)g(x_1|x_0)}{\pi_1(x_1)}$.
15 Then a sample value for x_2 is generated from another importance distribution with pdf
16 $\pi_2(x_2)$; an updated weight is calculated as follows: $w_2(x_1, x_2) = \frac{f(y_2|x_2)g(x_2|x_1)}{\pi_2(x_2)} * w_1(x_1)$. Repeat
17 until time T and resample the generated vectors with weights proportional to $w_T(x_1, \dots, x_T)$.
18 In the special case where $\pi_t(x_t) = g_t(x_t|x_{t-1}, \theta)$, the state pdf, the weight simplifies to the
19 observation pdf (“likelihood”) alone.

20 A variation on SIS called the Auxiliary Particle Filter (APF) (Pitt and Shephard 1999)
21 uses information about the state at time t provided by the observation at time t to generate
22 values and increase the efficiency (lower the Monte Carlo variation) of SIS.

23 To make inferences about unknown parameters θ (and the initial state x_0), Liu and West
24 (2001) extended the APF algorithm. At the beginning of the algorithm, values for θ are
25 generated from an “importance” distribution, e.g., the prior distribution for θ . The APF
26 algorithm involves resampling previously generated states, and in this case parameters, too,

1 every time period. Such a resampling reduces the number of unique parameter values (and
2 for that matter the number of unique values for previously generated states). This reduction,
3 also known as particle depletion, can lead to very high Monte Carlo variation. Liu and West
4 mitigate this depletion by kernel smoothing the parameter values, mixing the observed values
5 with a multivariate normal distribution with the same mean and covariance structure as the
6 observed values. If a retained particle has n copies following resampling, kernel smoothing
7 replaces those n duplicates with n slightly perturbed and usually unique values.

8 In our implementation of Liu and West’s algorithm we used the prior distributions for
9 generating the parameters and initial states. For a single set of hyperparameters for the
10 random effects, we generated ten unique random effects values so that potentially likely
11 hyperparameter values would be less likely to be removed early in the resampling process,
12 something that would be more likely if only a single random effect was paired with each
13 hyperparameter value. The degree of kernel smoothing was minimal, the weight given to
14 the observed value was 0.985. “Excessive” kernel smoothing can lead to the situation where
15 states early in the time series were generated from parameter values that have changed
16 considerably by the time states later in the time series are generated, thus introducing
17 considerable bias in the posterior distribution. Because all the parameters had uniform
18 priors and were thus restricted to finite line segments, the parameters were mapped to the
19 real number line for multivariate normal kernel smoothing, and then backtransformed after
20 kernel smoothing. Letting η denote the transformed value and θ the parameter on the
21 original scale, the mappings were as follows:

$$\begin{aligned} \eta &= \log(\theta - a)/(b - \theta) \\ \theta &= \frac{\exp(\eta)}{1 + \exp(\eta)}(b - a) + a, \end{aligned}$$

24 where $\theta \sim U(a, b)$.

25 To further reduce particle depletion, a more efficient resampling procedure known as

1 residual resampling (Liu and Chen 1998) was used, whereby a subset of particles is retained
 2 deterministically, i.e., those with relatively large weights are kept, and the remaining sample
 3 is drawn at random. Additionally, somewhat mimicking a procedure known as partial rejec-
 4 tion control (Liu et al. 2001), given an initial set of N particles, after year 1, a subsample of
 5 particles of size N_1 equal to the effective sample size, ESS (Liu 2001), was randomly selected
 6 according the weights at that time $w_1(x_1)$. This procedure was repeated until a desired
 7 number of particles was generated and the algorithm proceeded until the last time period
 8 when a random sample of size equal to the ESS at time T was drawn. The entire process
 9 was repeated until a final sample of approximately 120,000 was attained, a sample size with
 10 relatively negligible Monte Carlo variation, where the total number of initial particles was
 11 over 70 million.

12 The algorithm was implemented in C using random variate algorithms from Devroye
 13 (1986), the R project source code (<http://www.r-project.org>), and Press et al. (1992).
 14 On a Unix workstation with dual 2.66 GHz processors and 2 MB of RAM, an eventual
 15 sample of 120,000 could be generated in around 4 hours.

16 2.6 Pre-season prediction of juveniles

17 The juvenile production for year $T+1$ can be predicted pre-season using samples from the
 18 posterior distribution of the spawning escapement for year T , in particular samples of S_{2fT} ,
 19 S_{3fT} , and S_{4fT} , in combination with samples from the posterior distribution of the relevant
 20 parameters, namely α , β , and CV_{BH} . Given a posterior sample of size N of female returns
 21 for year T and the parameters, the juvenile production can be predicted from the following
 22 lognormal distribution.

$$\begin{aligned}
 23 \quad J_{T+1}^{*i} &\sim \text{Lognormal} \left(\log \left(\frac{F^{*i} \alpha^*}{1 + F^{*i} \beta^{*i} / 10,000} \right) - \frac{\sigma_{BH}^{2*i}}{2.0}, \sigma_{BH}^{2*i} \right) \\
 24 \quad F^{*i} &= S_{2fT}^{*i} \times \bar{E}_2 + (S_{3fT}^{*i} + S_{4fT}^{*i}) \times \bar{E}_{3,4}, \quad i = 1, \dots, N
 \end{aligned}$$

1 Adult returns can be estimated in a similar manner with the additional step of generating
2 the random effects for survival and maturation. Using information from 1992 through 2003,
3 predictions of both the juvenile outmigrants and adult returns were made for 2004.

4 **2.7 Other models for juvenile production**

5 Estimation of the juvenile production parameters, i.e., the Beverton-Holt spawner recruit
6 parameters, in the context of a SSM simultaneously accounts for autocorrelation in the time
7 series of spawners and recruits (juveniles) and measurement error. To determine the ef-
8 fect of this accounting for autocorrelation and measurement errors, the parameters of the
9 Beverton-Holt model were also estimated using maximum likelihood and Bayesian inference
10 using the bias-corrected lognormal model treating estimated female spawners (more precisely,
11 estimated eggs based on RBDD estimates and hatchery stray information) and estimated
12 juveniles as true values, and with autocorrelation ignored. The maximum likelihood esti-
13 mates (mles) were calculated using AD Model Builder (Otter Research Ltd., Sidney, BC,
14 Canada) and the Bayesian posterior means were estimated using WinBUGS (Spiegelhalter
15 et al. 2003) with the same priors as in the SSM (with a burn-in of 1000 and a chain length
16 of 40,000).

17 **3 Results**

18 **3.1 Parameter and random effects estimates**

19 The means and standard deviations of the posterior distributions for the parameters are
20 shown in Table 3 along with prior means. Density plots of the posterior and prior distribu-
21 tions of the parameters are shown in Figure 3.

1 The posterior distributions for the juvenile production parameters did differ noticeably
2 from the prior distributions though the shift in mean value was slight for the density depen-
3 dent parameter β . The α parameter can be interpreted as the expected survival rate from
4 eggs to fry and is estimated to be 0.64 on average.

5 As the table and figure both make clear, the data provide little information for estimating
6 age 3 and age 4 hyperparameters, namely, the hyperparameters for $\phi_{3,t}$, $\phi_{4,t}$, $\rho_{3f,t}$, and $\rho_{3m,t}$.
7 The posterior means for the random effects for survival did vary a moderate amount, while
8 the means for the age 3 and age 4 maturation rates varied only slightly. Figure 4 shows the
9 prior and posterior densities of some of the random effects parameters for a given year, and
10 the influence of the priors on $\phi_{4,t}$ and $\rho_{3m,t}$ is especially apparent. Given that estimates for
11 age 3 and age 4 returns are aggregated, it is not too surprising that these parameters are
12 difficult to estimate.

13 The data, however, did provide information about the age 2 hyperparameters for survival
14 and sex-specific maturation rates (Figure 3), and the resulting random effects (Figure 4).
15 The expected age 2 survival rates, $E[\phi_{2t}]$, is the same for the prior and posterior distributions,
16 namely 0.5%, but the variation in the distribution is less in the posteriors. The posterior
17 means for the random effects ϕ_{2t} ranged from 0.15% to 0.97%. The differences between sexes
18 in age 2 maturation rates were sizeable, consistent with salmon biologists's experience, with
19 the expected rates being 5.6% for females and 18.7% for males. The posterior means for
20 random effects ranged from 1.1% to 11.0% for ρ_{2ft} and from 14% to 30% for ρ_{2mt} .

21 The posterior means for coefficients of variation for the observations were 96%, 136%, and
22 109% for juveniles, M/R female returns, and RBDD ladder and fish trap returns. Theoretical
23 calculations of the CV for the estimated total adult return using RBDD data, based on the
24 variation in the percentage of the run observed after week 19, suggest a CV of around 125%.
25 The coefficients of variation are likely absorbing biases and model misspecification, however;
26 e.g., using a single value for all four estimates based on RBDD ladder and fish trap data is

1 likely incorrect.

2 **3.2 State estimates**

3 The posterior means for some of the state values are plotted along with the observations in
4 Figure 5. Since bias-corrected lognormal distributions were used, ideally, observations would
5 on average equal the posterior means. For juveniles and age 2 returns (combined males and
6 females) the fit is better than for the age 3 and 4 returns, possibly a reflection of using a
7 single coefficient of variation for all four categories of RBDD data. For the age 3 and age
8 4 females, for which there are two estimation procedures, the posterior means fall between
9 the two sets of estimates. Biases in one or both procedure are likely given the consistent
10 direction of the differences between them.

11 **3.3 One year ahead predictions**

12 Predicted values for year 2004 given 12 years of data (1992-2003) are shown in Table 4.
13 The considerable uncertainty in predicted values is evident from the relatively wide intervals
14 between the 5th and 95th percentiles, and the estimated values for each category fell within
15 these intervals. The predictive distributions were strongly right skewed and medians are
16 preferred over means.

17 **3.4 Alternative estimates for Beverton-Holt model parameters**

18 In Figure 6 the Beverton-Holt curves based on the mles and posterior means for α and β are
19 plotted. The comparison of mles with posterior means is confounded by the fact that the mles
20 correspond approximately to posterior modes, not means, assuming relatively uninformative
21 priors, and that the posterior distributions for β and CV_{BH} were right skewed. With these

1 cautions in mind, the mles for α , β , and CV_{BH} were 0.59, 0.00012, and 0.51, and the
2 posterior means from the non-SSM Bayesian analysis were 0.77, 0.00061, and 0.82 in contrast
3 to the SSM's posterior mean values of 0.63, 0.00088, and 0.59, with the differences in the
4 estimates of the density dependence parameter (β) particularly striking. Arguably, because
5 autocorrelation and measurement errors have been accounted for, the SSM's posterior means
6 are better estimates of the parameters of the assumed Beverton-Holt model.

7 4 Discussion

8 4.1 Multiple sources of uncertainty

9 The utility of state-space models is increasingly recognized in fisheries (Mendelssohn 1988;
10 Sullivan 1992; Speed 1993; Schnute 1994; Newman 1998 and 2000; Meyer and Millar 1999;
11 Millar and Meyer 2000; Schnute and Kronlund 2002; Rivot et al. 2004), ecology (Calder et
12 al. 2003; Clark and Bjornstad 2004), and wildlife (Besbeas et al. 2002; Thomas et al. 2005).
13 As emphasized by Schnute (1994) an advantage of SSMs over previously used statistical
14 procedures (for sequential fisheries data) is that SSMs account for both process variation as
15 well as observation (or measurement) error.

16 Process variation can be due to demographic or environmental variation. Hierarchical
17 SSMs readily incorporate environmental variation by introducing a third level to the SSM
18 whereby parameters of the state model, and possibly the observation model, are randomly
19 generated. The hyperparameters of this third level can potentially include environmental
20 covariates. Beta distributions were used for the survival and maturation probabilities; Rivot
21 et al. (2004) used the multivariate extension of the beta distribution, the Dirichlet, sim-
22 ilarly, for simultaneously accounting for survival and maturation to two different ages at
23 return. Logit-normal models for survival (Newman 2003) and maturation are an alternative

1 approach.

2 Putting the hierarchical SSM in a Bayesian framework adds a fourth level to the model
3 which allows for inclusion of prior beliefs about parameters and states. Additionally, the
4 resulting posterior distributions provide readily interpretable summaries of uncertainty about
5 parameters and states. In the case of weakly identifiable parameters, e.g., the age 3 and age
6 4 survival rates, we maintain that it is often better to incorporate uncertainty about their
7 values via the inclusion of prior distributions, than to fix the parameter values.

8 We did not address the issue of model uncertainty primarily because the SSM used
9 was closely patterned after what we considered to be a fairly realistic life history model.
10 However, alternative models could be, and have been, considered (see the Hallock and Fisher
11 model in Newman et al. (*in press*)). Model selection and model averaging for hierarchical
12 SSMs are topics for additional research. The use of information criteria, e.g., such as DIC
13 (Spiegelhalter et al. 2003), AIC (Burnham and Anderson 1998), BIC and Bayes Factors
14 (Kass and Raftery 1995), reversible jump Markov chain Monte Carlo (Green 1995), and
15 Bayesian model averaging (Hoeting et al. 1999) are potential approaches to addressing model
16 uncertainty, for selecting or averaging over models.

17 Lastly, the SSM framework easily allows inclusion of multiple sources of information
18 about the population components. The observation model is simply extended by adding
19 additional pdfs. In a case where a component of the state vector, say, is being estimated or
20 measured in two different ways and one procedure is thought to have a consistent bias while
21 the other is unbiased, both estimates can be included in the model by including a parameter
22 for that bias in the observation model. Thus indices of abundance can be included so long
23 as unbiased estimates exist, too. If the index is more precise than the unbiased estimator,
24 then that additional precision can be used advantageously. For example, suppose the RBDD
25 ladder-based estimates on average underestimate returns by some unknown fraction, but
26 the M/R estimates are unbiased. Then a parameter for this bias could be included and is

1 estimable; e.g., $E[y_{3+4f,t,RBDD}] = \psi(S_{3ft} + S_{4ft})$, where ψ reflects the bias. In the application
2 missing data from the different sources posed no serious problems and the model provided a
3 simple means of “imputing” the unobserved states, e.g., the 2001 and 2002 juveniles.

4 4.2 Fitting Bayesian hierarchical SSMs

5 Currently, there are two dominant methods for fitting Bayesian hierarchical SSMs, sequential
6 importance sampling (and its variants) and MCMC. One potential problem with MCMC
7 is that convergence to the posterior distribution can be difficult, given the frequent high
8 degree of correlation between states and parameters. In ongoing research with others we
9 have found that to make the MCMC sampler efficient, considerable thought is required
10 regarding the choice of proposal distributions, which parameters and/or states to update in
11 blocks, whether or not to insert auxiliary variables (states), and whether or not alternative
12 parameterizations are advisable. On the other hand, Rivot et al. (2004) successfully used
13 MCMC via the WinBUGS software (Spiegelhalter et al. 2003) for a relatively complicated
14 SSM, but noted (Etienne Rivot, personal communication) that the choice of initial values to
15 start the sampler was critical.

16 Implementation of sequential importance sampling is much simpler, especially when the
17 state pdfs are used as the importance samplers. The Liu and West (2001) algorithm is a rela-
18 tively straightforward procedure for making inferences about the states and the parameters,
19 and its inclusion of the auxiliary particle filter (Pitt and Shephard 1999) leads to a “better”
20 importance sampler but still one based on state pdfs. However, the main barrier to effi-
21 cient implementation of sequential importance sampling is particle depletion and subsequent
22 Monte Carlo variation. Kernel smoothing of parameters partially alleviates depletion of pa-
23 rameters (and could be used for states, too), but too much kernel smoothing will introduce
24 bias in the posterior distributions. Residual resampling and partial rejection control further

1 mitigate Monte Carlo variation. For this particular SSM we found our variation on partial
2 rejection control, whereby a good set of particles is sequentially accumulated, a pragmatic
3 means of reducing Monte Carlo variation.

4 The development of off-the-shelf software for fitting complex Bayesian hierarchical SSMs,
5 be it using MCMC or SIS or something else, would clearly be a valuable contribution.

6 **4.3 Evaluation of the winter chinook salmon model**

7 Criticism of the SSM implemented for the winter run chinook salmon can be categorized in
8 terms of the particular chosen model, including the prior distributions, and the type and
9 quality of data.

10 **Model formulation.** Beginning with the observation process model, in principal the raw
11 data could be the observations rather than the estimates. The sampling procedures are
12 relatively involved, however, with sampling covering an extended time period, both during
13 outmigration and during spawning migration, and to directly link observations made on a
14 weekly basis, for example, to the “available” state components is not easy. One would need
15 to extend the state model to include a migratory timing and/or spatial component for the
16 states. Given that estimates are used, the use of a single CV for all RBDD-based estimates
17 is clearly an oversimplification and could partly explain the systematic difference between
18 posterior means and estimates for age 3 and age 4 returns.

19 For the state process model, many alternative density dependent formulations are pos-
20 sible for juvenile production. The formulations can be divided into compensatory (e.g.,
21 Beverton-Holt) and overcompensatory (e.g., Ricker) dynamics. Barrowman et al. (2003) ar-
22 gue that for territorial fish such as coho salmon, compensatory dynamics are expected, and
23 they found that the Beverton-Holt stock-recruitment function provided a much better fit to

1 an extensive coho data set than the Ricker function. Because chinook salmon defend terri-
2 tories like coho salmon (Healey 1991 and references therein), we used Beverton-Holt density
3 dependence in our model. Incorporating covariates, such as water flow levels at time of fry
4 emergence (Speed 1993), could tighten the relationship between spawners and juveniles, too.
5 Alternative probability distributions could be used for the juveniles and the other states,
6 too. As mentioned previously, alternative models for the random effects for survival and
7 maturation include logit-normal models and the inclusion of year-specific covariates.

8 As for any Bayesian analysis alternative priors could be used. Uniform priors, while
9 restricted to a finite range, were a relatively conservative approach. However, we note that
10 for the random effects parameters the resulting prior distributions, beta distributions, were
11 somewhat more informative choices but the range of likely values was still relatively wide.

12 **Type and quality of data.** With regard to the type of data, separate estimates of age 3
13 and age 4 returns would clearly be advantageous. Age 3 and 4 survival parameters and age
14 3 maturation probabilities would be more identifiable. Additionally, if estimates continue to
15 be used as observations, standard errors need to be calculated in all cases; the inclusion of
16 estimate-specific standard errors would be less generic than a single coefficient of variation.
17 Somewhat less obvious, the way fish are sampled at the fish trap is somewhat similar to
18 temporally stratified multinomial sampling and non-zero covariances must exist between the
19 estimates of age 2 females, age 2 males, and so on, but these have been ignored. Currently,
20 however, standard errors, let alone covariances, are not currently available for the adult
21 return estimates (and only partially available for juvenile estimates).

22 With regard to quality of data, the juvenile estimates are in terms of fry equivalents
23 whereby fish over a certain length are classified as pre-smolts or smolts and a single fish is
24 expanded by a fixed value irregardless of when it was recovered. Arguably, time dependent
25 expansions would be an improvement. Run mis-identification is another problem. Three

1 other seasonal races of chinook salmon occupy portions of the Sacramento river system
2 during some of the same time periods. The identification of a returning salmon as being
3 winter run, instead of say a late fall run, is not an exact science and the degree to which
4 misclassification errors contribute to the observation noise is unknown.

5 **Use and advantages of the model.** We end on a more positive note by contrasting the
6 potential use of a Bayesian hierarchical state-space model with current management pro-
7 cedures. Currently, NOAA Fisheries, in its annual forecast of juvenile production, simply
8 multiplies the estimated spawning escapement by a factor that reflects the fraction of es-
9 capement that is female, average fecundity, and survival from egg to the delta, where the
10 pumps are located (Gaines and Poytress 2004). Prior to 2001, this factor was applied to
11 the RBDD estimates of escapement, but since then to the carcass-based M/R estimates. In
12 some years, juvenile production is directly estimated in-season from catches in rotary screw
13 traps, but funding vagaries prevented implementation in 2001 and 2002. Our method, with
14 its ability to incorporate multiple data sources with missing values, has made full use of all
15 of the relevant data in a consistent and statistically rigorous way. Additionally, the SSM
16 could be extended to include partial in-season juvenile catch information so that in-season
17 predictions could be used to modify or update the pre-season predictions.

18 The statistical foundations of our model allow calculation of valid interval estimates that
19 can provide managers with a context for assessing observed captures versus those predicted
20 by the model from the data. Prediction intervals for juvenile abundance (Table 4) show that
21 the forecasts contain a lot of uncertainty. Currently, managers have only point forecasts to
22 guide their actions. It is possible that under some hydrological conditions, a significantly
23 larger fraction of outmigrants could be impacted by pumping than is the case on average,
24 making it important to know whether observed catches at the pumps are consistent with
25 expectation or indicate a serious problem that might justify curtailing pumping.

1 We note that the forecasts of ocean abundance by age that our model produces are
2 potentially useful to managers of salmon ocean fisheries off California. A common method of
3 estimating ocean abundance of salmon prior to the fishing season is to use a linear regression
4 model that relates the returns of age a fish in year t to the returns of age $a + 1$ fish in year
5 $t + 1$ (Peterman 1982, Adkison and Peterman 2000). For winter chinook, by the time mature
6 age 2 fish are enumerated, the fishery has already impacted those fish destined to return
7 at age 3 the following year, and relatively few fish return at age 4. Such sibling regression
8 models are therefore not useful for winter chinook, and the only prospect for forecasting
9 ocean abundance is to base the forecast on spawner and juvenile data, although variability
10 in post-smolt survival may limit the usefulness of such forecasts (MacDonald et al. 1987).

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Table 1: Juvenile outmigrant and adult return estimates. The data sources are Gaines and Poytress (2004) and Bill Poytress (personal communication) for juveniles (in fry equivalents) and Doug Killam (personal communication) for adult estimates. These data, including straying hatchery female returns and egg and fork length data, are available electronically at <http://www.creem.st-and.ac.uk/ken/DATA/data.html>.

Obs'n Year	Juveniles (fry)	RBDD estimates				M/R estimates	
		Age 2f	Age 3f+4f	Age 2m	Ages 3m+4m	Age 2f	Ages 3f+4f
1992	NA	38	639	39	480	NA	NA
1993	NA	22	171	111	73	NA	NA
1994	NA	20	16	79	33	NA	NA
1995	NA	0	759	29	467	NA	NA
1996	1,816,984	65	402	564	175	NA	NA
1997	469,183	23	300	298	214	NA	NA
1998	2,205,162	385	1098	529	867	NA	NA
1999	5,000,416	559	428	1907	395	NA	NA
2000	1,366,162	172	344	517	172	NA	NA
2001	NA	218	959	3401	654	29	4655
2002	NA	366	3897	915	2720	42	5450
2003	8,205,609	315	2897	2522	2535	39	5226
2004	5,826,672	33	783	3784	1076	40	3260

Table 2: Hierarchical model for winter run chinook salmon. The notation $[\]$ indicates rounding to the nearest integer. The parameters σ^2 of the lognormal distribution are equivalent to $\log(CV^2 + 1)$. Other notation is given in text.

Prior pdfs for parameters

$$\alpha \sim U(0, 1.0)$$

$$\beta \sim U(0, 0.002)$$

$$CV_{BH} \sim U(0, 2.0)$$

$$\phi_{2a} \sim U(0.208, 2.892)$$

$$\phi_{2b} \sim U(41.264, 574.736)$$

$$\phi_{3a}, \phi_{4a} \sim U(0.134, 1.866)$$

$$\phi_{3b}, \phi_{4b} \sim U(0.201, 2.799)$$

$$\rho_{2fa}, \rho_{2ma} \sim U(0.214, 2.986)$$

$$\rho_{2fb}, \rho_{2mb} \sim U(1.943, 27.057)$$

$$\rho_{3fa}, \rho_{3ma} \sim U(0.402, 5.598)$$

$$\rho_{3fb}, \rho_{3mb} \sim U(0.268, 3.732)$$

$$\rho_{3ma} \sim U(0.402, 5.598)$$

$$\rho_{3mb} \sim U(0.268, 3.732)$$

$$CV_{\hat{j}}, CV_{\hat{A}-M/R}, CV_{\hat{A}-RBDD} \sim U(0, 2.0)$$

Hyperdistribution pdfs

$$\phi_{2t} \sim Be(\phi_{2a}, \phi_{2b}) \quad \phi_{3t} \sim Be(\phi_{3a}, \phi_{3b}) \quad \phi_{4t} \sim Be(\phi_{4a}, \phi_{4b})$$

$$\rho_{2ft} \sim Be(\rho_{2fa}, \rho_{2fb}) \quad \rho_{2mt} \sim Be(\rho_{2ma}, \rho_{2mb})$$

$$\rho_{3ft} \sim Be(\rho_{3fa}, \rho_{3fb}) \quad \rho_{3mt} \sim Be(\rho_{3ma}, \rho_{3mb})$$

Initial state pdf

continued on next page

Table 2: *continued*

$$F_{-j} \sim U(250 * 0.1, 2000 * 0.1) * \bar{E}_2 + U(250 * 0.9, 2000 * 0.9) * \bar{E}_{3,4}, \quad j = 4, 3, 2, 1,$$

$$\bar{E}_2 = 3025, \bar{E}_{3,4} = 6304$$

$$J_{-j} = \left[\frac{F_{-j-1} \alpha}{1 + \beta/10,000 F_{-j-1}} \right], \quad j = 3, 2, 1, 0$$

$$(O_{2f,-j}, S_{2f,-j}, O_{2m,-j}, S_{2m,-j}) \sim \text{Multinomial}(J_{-j-1}, 0.5\phi_{2,-j}(1 - \rho_{2f,-j}),$$

$$0.5\phi_{2,-j}\rho_{2f,-j}, 0.5\phi_{2,-j}(1 - \rho_{2m,-j}), 0.5\phi_{2,-j}\rho_{2m,-j}), \quad j = 2, 1, 0$$

$$(O_{3f,-j}, S_{3f,-j}) \sim \text{Trinomial}(O_{2f,-j-1}, \phi_{3,-j}(1 - \rho_{3f,-j}), \phi_{3,-j}\rho_{3f,-j}), \quad j = 1, 0$$

$$(O_{3m,-j}, S_{3m,-j}) \sim \text{Trinomial}(O_{2m,-j-1}, \phi_{3,-j}(1 - \rho_{3m,-j}), \phi_{3,-j}\rho_{3m,-j}), \quad j = 1, 0$$

$$S_{4f,0} \sim \text{Binomial}(O_{3f,-1}, \phi_{4,0})$$

$$S_{4m,0} \sim \text{Binomial}(O_{3m,-1}, \phi_{4,0})$$

State process pdf

$$F_t = (S_{2f,t-1} + H_{2f,t-1}) * \bar{E}_2 + (S_{3f,t-1} + S_{4f,t-1} + H_{3+4,f,t-1}) * \bar{E}_{3,4}$$

$$J_t \sim [\text{Lognormal}] \left(\log \left(\frac{F_{t-1} \alpha}{1 + \beta/10,000 F_{t-1}} \right) - \frac{\sigma_{BH}^2}{2}, \sigma_{BH}^2 \right)$$

$$(O_{2ft}, S_{2ft}, O_{2mt}, S_{2mt}) \sim \text{Multinomial}(J_{t-1}, 0.5\phi_{2t}(1 - \rho_{2ft}), 0.5\phi_{2t}\rho_{2ft}, 0.5\phi_{2t}(1 - \rho_{2mt}), 0.5\phi_{2t}\rho_{2mt})$$

$$(O_{3ft}, S_{3ft}) \sim \text{Trinomial}(O_{2f,t-1}, \phi_{3t}(1 - \rho_{3ft}), \phi_{3t}\rho_{3ft})$$

$$(O_{3mt}, S_{3mt}) \sim \text{Trinomial}(O_{2m,t-1}, \phi_{3t}(1 - \rho_{3mt}), \phi_{3t}\rho_{3mt})$$

$$S_{4ft} \sim \text{Binomial}(O_{3f,t-1}, \phi_{4t})$$

$$S_{4mt} \sim \text{Binomial}(O_{3m,t-1}, \phi_{4t})$$

Observation process pdf

$$y_{Jt} \sim \text{Lognormal} \left(\log(J_t) - \frac{\sigma_J^2}{2}, \sigma_J^2 \right)$$

$$y_{S-RBDD,ast} \sim \text{Lognormal} \left(\log(S_{ast}) - \frac{\sigma_{\hat{A}-RBDD}^2}{2}, \sigma_{\hat{A}-RBDD}^2 \right) \quad a = 2, 3 + 4, \quad s = f, m,$$

$$y_{S-M/R,ast} \sim \text{Lognormal} \left(\log(S_{aft}) - \frac{\sigma_{\hat{A}-M/R}^2}{2}, \sigma_{\hat{A}-M/R}^2 \right) \quad a = 2, 3 + 4$$

Table 3: Posterior means and standard deviations for parameters of winter run chinook salmon SSM based on observation years 1992-2004.

Parameters	Prior	Posterior		
	Mean	Mean	Median	SD
α	0.50	0.63	0.62	0.18
β	0.001	0.00088	0.00080	0.00053
CV_{BH}	1.00	0.59	0.47	0.45
ϕ_{2a}	1.55	1.73	1.71	0.56
ϕ_{2b}	308	378	393	133
ϕ_{3a}	1.00	1.18	1.20	0.39
ϕ_{3b}	1.50	1.48	1.46	0.74
ϕ_{4a}	1.00	1.08	1.11	0.48
ϕ_{4b}	1.50	1.48	1.45	0.75
ρ_{2fa}	1.60	1.14	1.04	0.51
ρ_{2fb}	14.50	19.5	20.7	5.36
ρ_{2ma}	1.60	2.23	2.32	0.51
ρ_{2mb}	14.50	9.66	8.01	5.91
ρ_{3fa}	3.00	3.59	3.77	1.36
ρ_{3fb}	2.00	2.07	2.08	0.97
ρ_{3ma}	3.00	3.32	3.42	1.41
ρ_{3mb}	2.00	2.01	2.03	0.92
CV_j	1.00	0.95	0.90	0.47
$CV_{\hat{A}-M/R}$	1.00	1.44	1.47	0.36
$CV_{\hat{A}-RBDD}$	1.00	1.08	1.03	0.33

Table 4: One year ahead predictions for 2004 based on posterior distributions of states and parameters estimated from 1992-2003 data (based on SIS with 120,000+ particles). The first lines for each state show the predictions without observation error. The second (and third) lines contain the percentiles with observation error; estimated females with observation error included are listed separately for the RBDD ladder counts and the M/R estimates.

Juveniles (1000s)				
2004 Estimate	Expected Value	Prediction Percentiles		
		5th	50th	95th
	5,688	1,020	4,311	13,929
5,827	5,688	385	3,133	17,783
Age 2 Females				
2004 Estimate	Expected Value	Prediction Percentiles		
		5th	50th	95th
	1,257	13	466	4,891
(RBDD) 33	1,257	8	314	5,046
(M/R) 40	1,257	4	223	4,354
Age 2 Males				
2004 Estimate	Expected Value	Prediction Percentiles		
		5th	50th	95th
	3,926	121	1,845	14,211
(RBDD) 3,784	3,985	60	1,255	15,131
Age 3+4 Females				
2004 Estimate	Expected Value	Prediction Percentiles		
		5th	50th	95th
	4,274	353	2,816	12,877
(RBDD) 783	4,274	156	1,918	15,266
(M/R) 3,260	4,274	98	1,497	16,374
Age 3+4 Males				
2004 Estimate	Expected Value	Prediction Percentiles		
		5th	50th	95th
	3,291	256	2,092	10,242
(RBDD) 1,076	3,291	116	1,433	11,730

Figure 1: Sacramento River and major dams. Historical spawning areas for winter run chinook salmon included rivers above Shasta Dam.

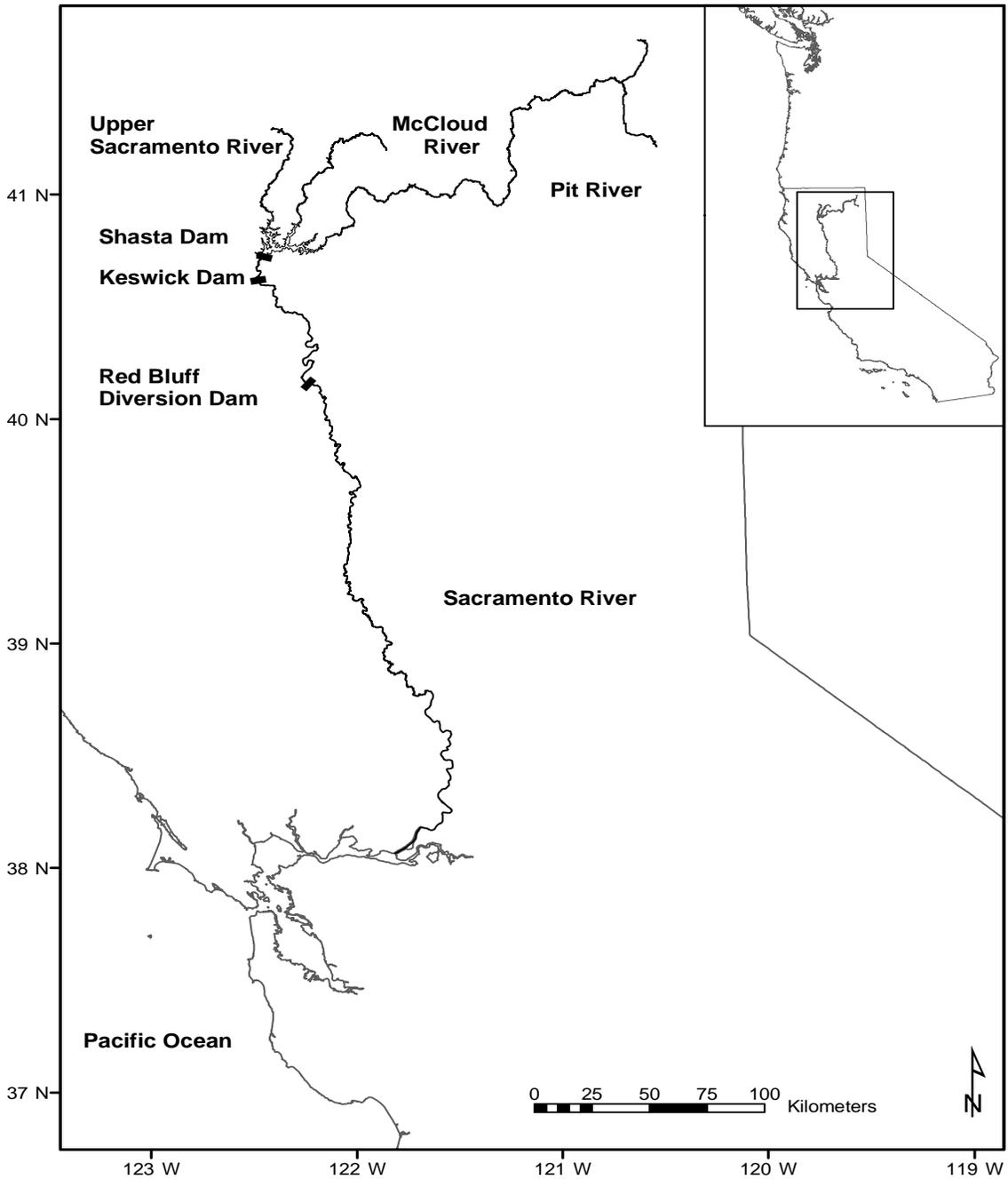


Figure 2: Schematic of winter-run chinook salmon life history. S denotes spawners with subscripting for age, sex, and year of spawning, J are juveniles, while O are immature fish remaining in the ocean. The parameters ϕ denote survival (age-specific), the ρ s are age- and sex-specific maturation probabilities, and p_m is the probability of a fish being male.

	Numbers		Numbers		Numbers		Numbers
Year $t-1$	Year t	Processes	Year $t+1$	Processes	Year $t+2$	Processes	Year $t+3$
	(Males)	$\phi_{2,t+1} \xrightarrow{p_m} \rho_{2m}$	$S_{2m(t+1)}$	$\phi_{3} \xrightarrow{\rho_{3m}}$	$S_{3m(t+2)}$		
		$\phi_{2,t+1} \xrightarrow{p_m} (1 - \rho_{2m})$	$O_{2m(t+1)} \begin{matrix} \nearrow \\ \searrow \end{matrix}$	$\phi_{3} \xrightarrow{(1 - \rho_{3m})}$	$O_{3m(t+2)}$	$\xrightarrow{\phi_4}$	$S_{4m(t+3)}$
$S_{2f(t-1)} \searrow$	$J_t \begin{matrix} \nearrow \\ \searrow \end{matrix}$						
$S_{3f(t-1)} \rightarrow$		$\phi_{2,t+1} \xrightarrow{(1 - p_m)} \rho_{2f}$	$S_{2f(t+1)}$	$\phi_{3} \xrightarrow{\rho_{3f}}$	$S_{3f(t+2)}$		
$S_{4f(t-1)} \nearrow$	(Females)	$\phi_{2,t+1} \xrightarrow{(1 - p_m)} (1 - \rho_{2f})$	$O_{2f(t+1)} \begin{matrix} \nearrow \\ \searrow \end{matrix}$	$\phi_{3} \xrightarrow{(1 - \rho_{3f})}$	$O_{3f(t+2)}$	$\xrightarrow{\phi_4}$	$S_{4f(t+3)}$

Figure 3: Posterior (solid lines) and prior (dashed) densities of the parameters. Vertical lines mark the posterior means. Posterior densities are based upon 120,000+ particles.

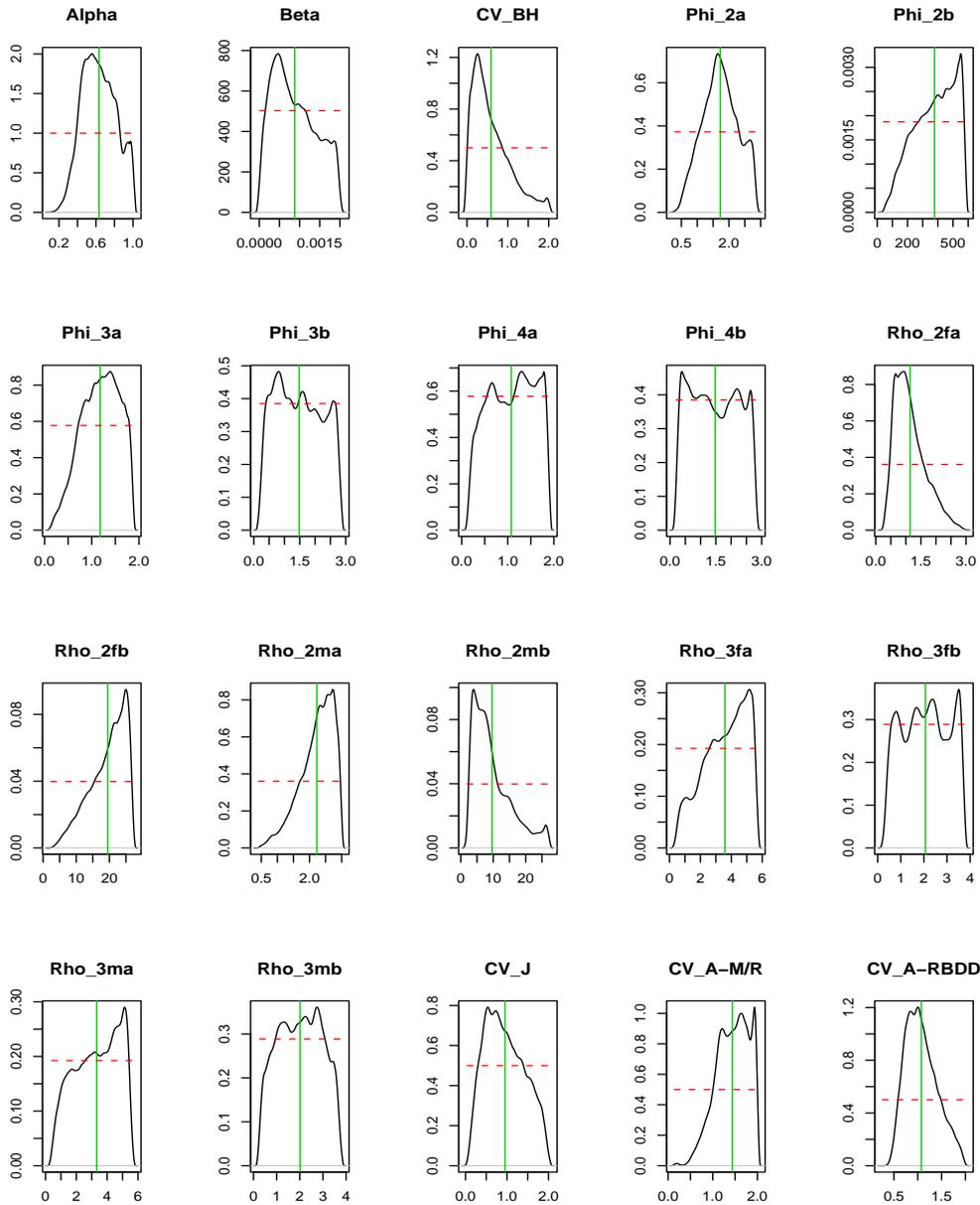


Figure 4: Posterior (solid lines) and prior (dashed) densities of random effects for 1998. Posterior mean values are shown above each plot. Posterior densities are based upon 120,000+ particles.

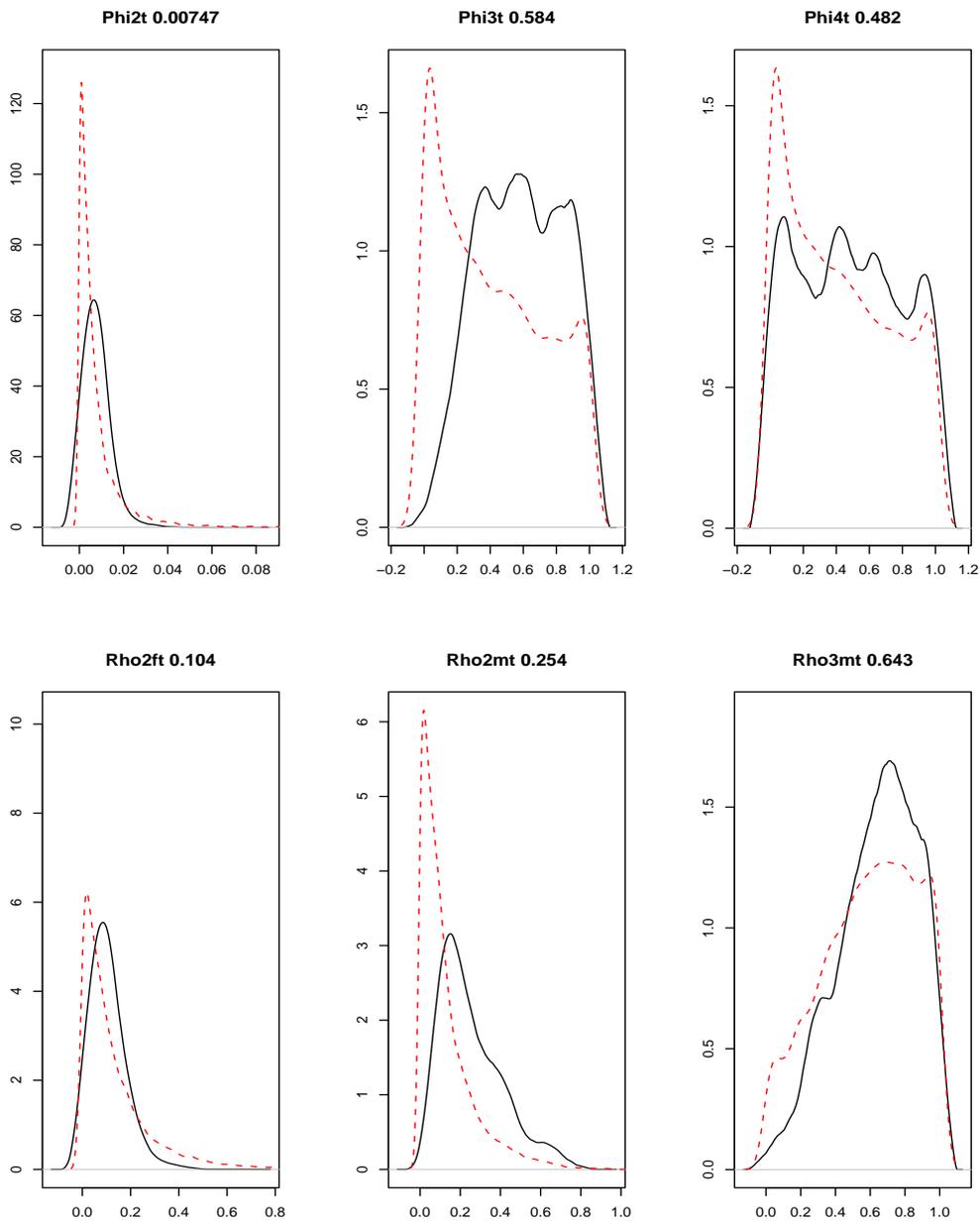


Figure 5: Posterior means (solid lines) for states along with observations (dashed lines). The age 2 returns are the sum of male and female returns, as are the age 3 and 4 returns. The dotted line in the bottom plot, for age 3+4 females, shows the M/R estimates of females.

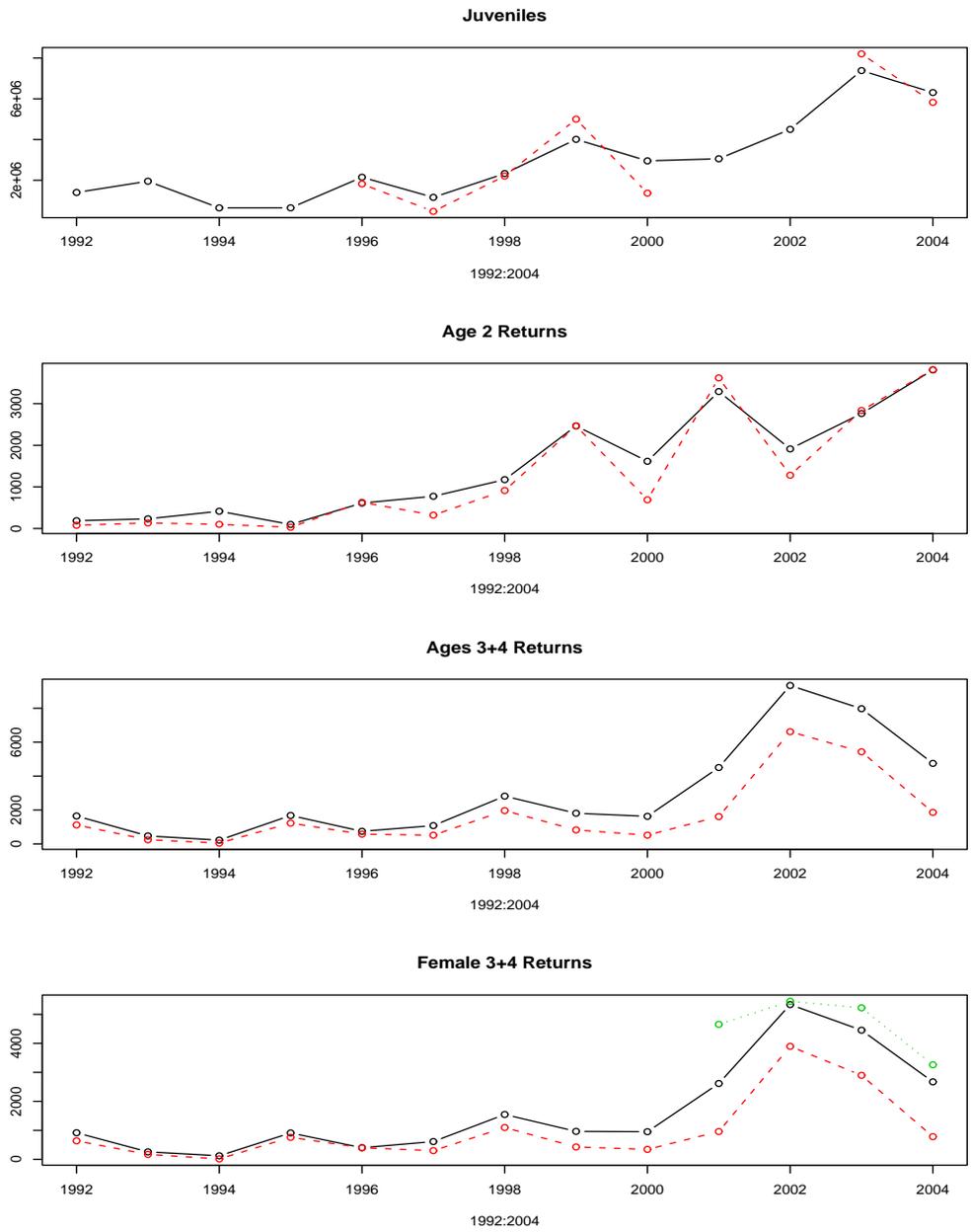


Figure 6: Fitted Beverton-Holt spawner-recruit curves, $Juv = \frac{\alpha Eggs}{1 + \beta/10,000 * Eggs}$, based on posterior means from the SSM (solid line), the posterior means from a Bayesian analysis ignoring autocorrelation and measurement errors (dotted line), and maximum likelihood estimates based on a bias-corrected lognormal distribution (dashed line). The juvenile estimates (7 years) are shown as circles and the SSM posterior means for juveniles (13 years) are shown as triangles.

